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Ecological factors affecting the distribution of freshwater fishes in tropical Southern Africa

It is a *sine qua non* that, if a fish is to live, it must have water. It is not sufficient, however, to consider the distribution of freshwater fishes entirely in terms of the amount of water in the form of lakes, rivers, streams and marshes that are now, or have been in the past, available to make the existence of fishes in them physically possible. As well as the physical factors inherent in the sheer existence of water, there are also ecological factors which affect the distribution of fishes. I do not propose in this short paper to discuss very much the physical factors of the availability of water, watersheds, barriers and so forth. While much remains to be done, such aspects of the distribution have been discussed (for the area in question) by, among others, Worthington (1933), Ricardo (1943), de Beaufort (1951) and Poll (1957). Comparatively little is known, however, of the ecological factors involved, and it is the main purpose of the present paper to discuss some of these aspects.

The fresh waters of tropical southern Africa include two large Rift Valley lakes, Tanganyika and Nyasa, a series of smaller lakes, and a wide range of rivers, streams, swamps and marshes. Fishes are widely distributed in these, very often discontinuously, and it is clear that ecological factors play a large part in this distribution. We are very far from having even an empiric knowledge of each fish; when we do, many of the present difficulties confronting the student of distribution will probably fall away.

At the beginning of a fish's life, as egg, alevin or fry, it seems that the most important ecological requirements of this stage are cover, a refuge from predators, and food. The theory has been put forward by Jackson (1961b) that, in order to place the eggs and young in an environment where these requirements can be met, parent fishes undertake an annual spawning migration. Even in our present limited state of knowledge a list of such known spawning migrations is impressive. The movement is always upstream, and known migrations include both extended movements up large rivers into smaller tributaries, swamps and flood-plains, and also many cases of anadromesis from large lakes into affluent rivers. As Whitehead (1959) has remarked, migrating fishes must have the ability to tolerate a wide range of environmental conditions, such as, in the case of anadromous fishes, those that exist between river and lake.

It can be seen that we have here a case where ecological factors can affect distribution. While the urge to migrate may be primarily for spawning and, according to Jackson's (1961b) theory, motivated primarily by the powerful urge to place the eggs and young in an environ-

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ment most suited for their survival, it can readily be seen that the very fact that such a strong migratory urge exists is in itself a potent mechanism for the distribution of freshwater fishes. Species of fish which undertake long and often arduous migrations at regular intervals are *ipso facto* in a good position to colonize new waters when these become available, as, for example, when a river changes its course or a barrier breaks down in the course of geological time.

The position of such migratory species may be contrasted with that of the species which exist, often in species-flocks of closely related species, in the Great Lakes of Africa, such as (in the area under review) lakes Nyasa and Tanganyika, and are endemic, each to a particular lake. It is a remarkable fact that these endemic species do not migrate out of the lake up rivers to spawn to anywhere near the same extent as do those which are either non-endemic or are closely related to a more widely distributed species. In discussing this phenomenon with regard to the anadromous fishes of Lake Victoria, Whitehead (1959) has this to say (p. 343): "Amongst the anadromous fishes of Lake Victoria speciation nowhere approaches the level found for example in the static cichlid species of the lake. The anadromous fishes . . . are able to overcome large micro-environmental barriers in temperature, substrate, feeding possibilities, etc., barriers which appear to isolate many of the more specialised lake forms."

It thus seems possible to reach the following conclusion with regard to the distribution of fishes in tropical southern Africa. This is that distribution over wide areas of the subcontinent is limited to those unspecialized fishes of migratory habit which are not endemic to a lake. The narrower ecological requirements of the lake endemics appear, in our present state of knowledge, to make it impossible for them to distribute themselves in any water, no matter how adjacent, other than that lake to which they are endemic. There are dozens of genera and hundreds of species, especially though not exclusively of the family Cichlidae, known from Lake Tanganyika and Lake Nyasa, but, apart from those anadromous fishes closely related to species outside which are mentioned above, no records exist of any of these endemics being found in rivers, marshes, etc., even where no large barriers exist and non-endemic fishes from the same lake are known to migrate there.

It has long been known (Trewavas, 1949) that these endemic lake species are often beautifully adapted to individual very definite environments within the lake. Such adaptations are very often reflected in the dentition, which in the various species is modified to various feeding habits. It seems that these and other specializations preclude the lake endemics from distributing themselves more widely. The question of their distribution into suitable micro-environments within their parent lake is in itself a problem which falls into the scope of the present paper, but time does not allow it to be further discussed.

The suitability of the environment is, of course, all-important. A special aspect of the question of ecological factors affecting the distribution of freshwater fishes is the case of the environment becoming, in the course of time, unsuitable for a particular species, which then dies out in the area affected by the change. Such cases are well known in general, but have been little studied in freshwater fish, amongst which our knowledge of taxonomy and ecology has mostly been insufficient to allow of work on this question.

One such problem is that of the distribution of the large-mouth "bream" *Serranochromis robustus* (Gunther) in the Zambezi system. The question here is that this well-known species occurs in suitable habitats in Lake Nyasa and the Upper Shiré River, and was originally described from this area. But what is, in the present state of our taxonomic knowledge, considered to be the same species, any known differences being thought to be of subspecific importance at most, occurs again in the Upper Zambezi Okovango/Kafue area. It is not known from anywhere along the Zambezi River in between. This case of discontinuous distribution, where the Murchison Cataracts on the Shiré River are separated from the Victoria

Falls on the Zambezi by a water distance of approximately 1,500 km., has puzzled taxonomists who found it difficult to recognize the same species from two such widely separated areas.

It is possible that this question may be resolved, at least in part, by considering some of the ecological factors involved. *S. robustus*, like all other members of the genus, has a distinct preference for water in which there is a good deal of aquatic vegetation; it is, in fact, a fish of those rivers for which I have in an earlier paper (Jackson, 1961a) proposed the term "reservoir" rivers. No case is known of a *Serranochromis* species inhabiting the other broad class of river, the "sand-bank" river of which the Middle Zambezi was, before the advent of Kariba, a typical example. Here the river, in contrast to the often marshy and always well-grown Upper Zambezi, dwindled to a comparative trickle between sand-banks during the dry season, with very little aquatic vegetation. Thus it is probable that the reason why *Serranochromis robustus* was absent from the long length of the Middle and Lower Zambezi was that conditions were ecologically unfavourable for it here during a large part of the year.

Now it is possible to postulate that this was not always so. It is possible that, at some past pluvial period, higher rainfall and reservoirs of water flowing into the Middle Zambezi made it more like the Upper Zambezi than it is now, so that *S. robustus* was able to inhabit the whole length of the river. When these favourable conditions came to an end, the fish was no longer able to exist in the middle and lower reaches, thus breaking the link between the populations in the Upper Zambezi and Upper Shiré. Weight may be added to this theory by the fact that, though the fish is absent from the Middle Zambezi River, occurrences of a *Serranochromis* have been reported from isolated parts of the Kalomo and Luansemfwa rivers, both of which flow into the Middle Zambezi. If such isolated populations do occur here, they may be remnants, which have survived in a favourable place, of a once much more extended population which at one time existed along the length of the Zambezi.

Worthington (1933) favoured also the view that communication between the Nyasan and neighbouring faunas took place along the Zambezi, but via the Kafue, which, after a tortuous course, enters the Middle Zambezi some 480 km. below the Victoria Falls. Here, again, past favourable conditions must have occurred to make the Middle and Lower Zambezi ecologically habitable for such species as *Serranochromis robustus* from this point down. An alternative theory, which can imply that *S. robustus* was never at any time in the middle and lower reaches of the Zambezi, is also mentioned by Worthington (*ibid.*, p. 288, footnote). This records that Captain C. R. S. Pitman had observed a definite channel of communication between the Rhodesian Congo and the Zambezi, between the upper reaches of the Luapula (Chambezi) and the Luangwa rivers. For *S. robustus*, the line of communication in this case would be from the Upper Zambezi Kafue through the Rhodesian Congo (where it is known) then into the Luangwa. From the Luangwa a similar process might have led to the fish entering the headwaters of some of the rivers which enter northern Lake Nyasa, such as the Songwe and the North Rukuru. Again, however, the ecological factor comes in, and it is necessary to postulate a more favourable environment in the past, because the Luangwa River to-day is one of the sand-bank rivers of Africa, and *S. robustus* is not known to occur in it.

The case of one species of fish has been put forward in some detail to illustrate the point that ecological preferences of a species must be understood in order to elucidate problems regarding its distribution. In general, ecological factors affect distribution in many ways. One factor very important in freshwater fishes is that of water temperature. Most tropical fishes are limited in distribution by being very sensitive to a temperature drop. Thus the widespread *Tilapia mossambica* Peters in its southward distribution becomes more and more limited to the lower altitudes nearer the sea until it is finally confined to river mouths and brackish lagoons along the north-eastern South African seaboard. On the other hand some species, such as the Mountain Catlet *Amphilius platychir* Gunther, are even in the most tropical parts of our region confined to cooler upland streams. Another factor is the need for cover, especially for smaller species which are more liable to predation by, e.g., the tiger-fish *Hydrocyon vittatus* Castelnau, than are those which reach a fairly large size when adult. In this regard Jackson (1961b) gives a table showing that the number of fish species known from the Middle Zambezi is very considerably less than those which are known from the adjacent Kafue and Upper Zambezi systems. Moreover, only 28·6 per cent of the Middle Zambezi fishes grow to a length less than about 18 cm. when adult, as against 55·5 per cent from the Upper Zambezi and 65·5 per cent from the Kafue, where there is better growth of aquatic vegetation all the year round.

The wide distribution of the top-minnows of the family Cyprinodontidae in tropical southern Africa can be explained by their small size and ability to colonize and live in the shallowest of waters, provided conditions of temperature are suitable and there is sufficient aquatic vegetation. One genus of the family, the brightly coloured *Nothobranchius* Peters, takes its adaptability to adverse physical conditions farther than most in that it is believed (Vanderplank, 1941) that eggs are laid which are drought-resistant, and can remain alive in the mud of a dried-up swamp until the advent of rain refills the swamp with water. It is clear that fish with this ability are well equipped to survive when other fish could not, a fact conducive to wide distribution.

I may finally stress that it is the eurytropic fish, able to tolerate a range of habitat, that is at once most likely to have a wide range of distribution and least likely to show any marked discontinuity. In general, the family Clariidae afford a wide range of examples and fields for further study. The genera and subgenera of this single family exhibit every phase, which is more or less accurately reflected in their distribution, from the widest ecological tolerance to the narrowest specialization. Much rests here on the development and use of the suprabranchial organ, which permits existence in foul or very muddy water. Species of the subgenus *Clarias* (*Heterobranchiodes*) have a wide and continuous distribution of the clinal type, so that it is extremely difficult to identify the species where the range of one species ends and that of the next begins. Thus *Clarias* (*H.*) *gariepinus* (Burchell) merges almost imperceptibly into *C.* (*H.*) *mossambicus* Peters, which again, further north, can scarcely be distinguished from *C.* (*H.*) *lazera* C. & V. where the ranges of the two overlap. The subgenus *Clarias* (*Clarias*) is considerably less catholic: the factor of temperature, among others, restricts its distribution, and only one species of this subgenus, *C.* (*C.*) *theodorae* Weber has a really wide distribution. The genus *Heterobranchus* Geoffroy is largely limited to large rivers and lakes, and there are other genera and subgenera, e.g. *Clariallabes* Boulenger, even more restricted.

One of the most remarkable of these groups are those restricted, and endemic to, lakes Nyasa and Tanganyika. A species-flock of endemic clariids is known from Lake Nyasa (Jackson, 1959), but only one from Lake Tanganyika. These behave in the same way as do other endemic forms in these lakes, being specialized to a narrow micro-environment and never being found even in affluent rivers where no large barriers exist. Greenwood (1961) shows that in these Rift Lake endemics the suprabranchial organs which are so strongly developed in the more eurytropic and widely distributed members of the family, are in all cases poorly developed and in some, entirely absent. From the point of view of distribution, however, the most remarkable of Greenwood's (*op. cit.*) findings is that, on morphological grounds alone, the single Tanganyikan species and the Nyasan species-flock are anatomically so alike that they should all be referred, in his opinion, to the single genus *Dinotopterus* Boulenger. This provides a most difficult problem in the field of animal distribution in southern Africa. How it is that of all the genera endemic to either one of these two widely separated lakes, this one alone has succeeded in colonizing both is a puzzle in distribution that no one yet has attempted to explain.

It is well to end on a note of puzzlement, because there are problems enough in the distribution of fish to make the field a stimulating one for the student of animal distribution. A single member of the genus *Bagrus* Cuvier, *B. meridionalis* Gunther, occurs in Lake Nyasa and the Upper Shiré, but is absent from the Zambezi system, the Rhodesian Congo or Lake Tanganyika, the genus not otherwise occurring nearer than the large lakes and eastward-flowing rivers of East Africa. An endemic species-flock of the genus *Chrisichthys* Bleeker exists in Lake Tanganyika; there is only one, separate, species in the lakes and large rivers of the Rhodesian Congo and the genus is absent from any part of the Zambezi Kafue system or Lake Nyasa. Finally the distribution of the well-known electric catfish *Malapterurus electricus* Gmelin is markedly discontinuous in the area under review, for some reason as yet unknown. There is a belt, extensively watered, right across the sub-continent in which it does not occur. North of the belt it occurs in the Middle Congo and Lake Tanganyika. In the belt itself it is absent from the Upper Zambezi and Kafue, the Rhodesian Congo, including lakes Mweru and Bangweulu, and Nyasaland, including Lake Nyasa. Below the belt it reappears again in the Middle and Lower Zambezi and the Pungwe.

The above examples show that much remains to be discovered, but it nevertheless seems clear that it is not sufficient to take only physical characters of the environment into consideration. Important and indeed essential as these are, there are also ecological factors to be considered which may in some cases prove to be of as great importance. Environmental factors, such as for example a waterfall, may prove to be a barrier to a whole range of species belonging to several families, but ecological factors are more individual. The understanding of them necessitates research into the ecology of individual species; it may be, when such research has been done and the ecology of individual species better known, that the knowledge we have gained will contribute to a greater extent than we perhaps appreciate at present to our knowledge of the problems of animal distribution.

Summary

Ecological factors are probably as important as environmental factors in governing the distribution of fish in tropical southern Africa. These factors are more individual in their effect on either restricting or extending distribution than are environmental factors. A waterfall may form a barrier to a large number of species, but a preference for weedy conditions may restrict only one of these. Examples are given of ecological tolerances operating both to extend the range or limit the distribution of various species. In an as yet unexplained case of discontinuous distribution along the Zambezi, it is postulated that changes in the environment put part of the area outside the range of ecological tolerance of the species concerned. Endemic lacustrine species, ecologically restricted to a narrow habitat, are less likely to have a wide distribution than are those species with a wider ecological tolerance.

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DISCUSSION

Prof. Balinsky: There is a need for sharper definition of the terms used in zoogeographical work. This paper, for instance, distinguishes between ecological factors and environmental factors, which most workers would regard as one and the same thing.

Dr. Winterbottom: Jackson states that the fish fauna of the upper Zambezi is much richer than the middle and lower reaches, but I would like to know how many species are common to both areas. The author classifies the middle and lower Zambezi as a "sandbank river", but the upper Zambezi is also a "sandbank river" in the dry season although, because it flows through flood plains, it has creeks and lagoons which provide additional and different environments.

Dr. Talbot: This is Mr. Jubb's work, but, as far as I remember it, there is an almost complete discontinuity between the upper and middle Zambezi.

Mr. Attwell: I do not altogether agree with Dr. Winterbottom regarding the upper Zambezi, which, I think, provides a much richer environment than the typical sandbank rivers.